

# An allometric method for the projection of eelgrass leaf biomass production rates

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## ABSTRACT

We demonstrate that an allometric model for eelgrass leaf-growth rates can be derived from data on leaf architecture and growth form. Using this construct, we produced indirect assessments of growth rates of leaves that we call projections, which can be easily obtained in terms of allometric parameters and proxy values for leaf area, expressed as the product of leaf length and width. These projections of leaf-growth rates displayed a high level of correspondence with values observed in our data, as well as with other sets of reference data. A comparison with growth rates obtained by using the plastochrone index method showed that our model provides more accurate estimations while using a simpler methodology. Our results also show that whenever allometric parameters for the scaling of eelgrass leaf dry weight in terms of leaf area are available, the proposed model provides an accurate, cost-effective and non-destructive alternative to assessments based on traditional or plastochrone methods.

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## 1. Introduction

Constanza et al. [1] stressed the relevance of ecosystems services as a contribution to human welfare. Based on published data for 17 ecosystem services in 16 biomes, they estimated that the value of ecosystem services at the level of the whole biosphere. They found a lower bound in the range of US\$16–54 trillion ( $10^{12}$ ) per year with an average of US\$33 trillion per year. Marine systems contributed about 63% of the annual value, with almost half deriving from coastal systems. Approximately 25% of the overall contribution of coastal ecosystems corresponded to algal beds and seagrasses, which are submerged angiosperms that are considered a characteristic feature of shallow environments in tropical and temperate zones.

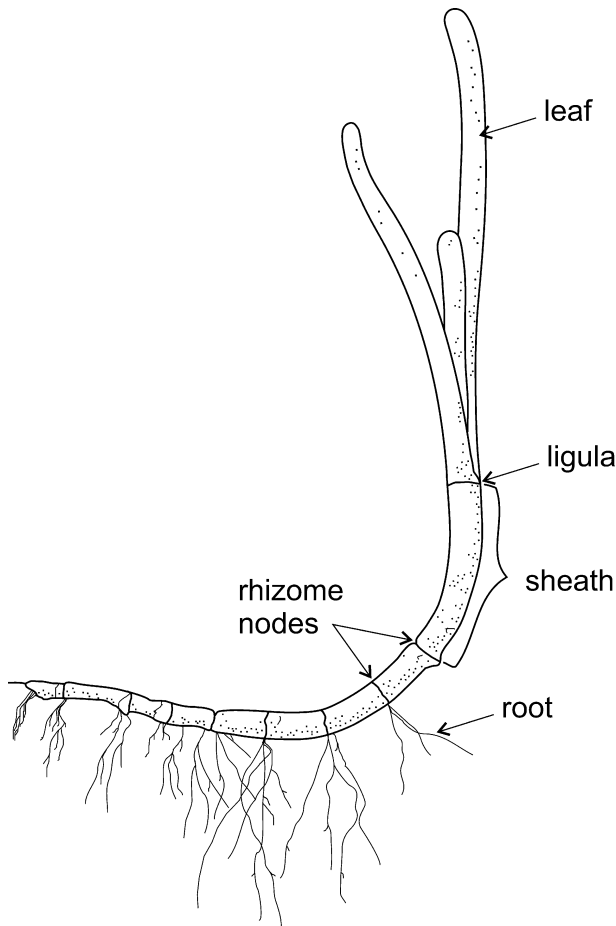
Petersen [2,3] pioneered research aimed at characterizing the ecological relevance of seagrass species. His studies provided groundbreaking perspectives on the functional attributes of seagrasses, emphasizing their role as vigorous primary producers. Nonetheless, half a century passed before marine scientists fully acknowledged that seagrass meadows are among the most productive ecosystems, rivaling tropical agriculture [4–10]. Although high primary productivity is a key feature in the trophic role of seagrass meadows [11–13], they also furnish an essential structural element by providing habitat for the growth of epiphytes [14,15] and shelter for animal communities [16,17]. Seagrasses are thus not only useful indicators of the health status of coastal zones,

but also their ability to modify their own environment, particularly in relation to the processing of sediments, allows them to be used in coastal management strategies aimed at preserving or improving environmental quality. It is this important attribute that has granted them the title of ecosystem engineers [18–21]. Nevertheless, it is their contribution to nutrient cycling within estuaries which represents the largest proportion of the economic benefit performed by seagrass meadows [22–24,1].

Eelgrass (*Zostera marina* L.) is a particularly appropriate species for the study of seagrass ecology, not only because it is the dominant species along the coasts of both the North Pacific and North Atlantic [25], but also because eelgrass communities are recognized as among the richest and most varied in the abundance of sea life [26]. Indeed, this cosmopolitan macrophyte was found to produce up to 64% of the total primary production of an estuarine system [27]. Therefore, the assessment of eelgrass biomass variability through time provides valuable information on the dynamics of both its trophic and structural roles. The basic unit for studying biomass production in eelgrass is the shoot (see Fig. 1), which includes leaves, rhizomes and roots. A rhizome is a horizontal stem that grows along the sediment, forming roots as it elongates. Root emergence occurs at leaf scars, also known as rhizome nodes. Leaves appear from a meristem lying within a protective sheath. This structure also holds the leaves together and is attached at the actively growing end of the rhizome. The production of leaves and rhizome nodes is linked in such a way that every leaf produced is associated with a rhizome node. Hence, the overall production of shoots can be estimated by measuring the production of leaves [28], which makes the determination of the growth rate of leaves a fundamental entry for the assessment of eelgrass

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**Fig. 1.** A pictorial representation of an eelgrass shoot. The segmented stem portrayed is called a rhizome. Each segment is bounded by nodes also called rhizome scars. These nodes are produced when new leaves are formed. The bundle of leaves is attached to the sheath, a specialized structure located at the end of the rhizome which contains a meristem where new leaves are produced. This drawing was adapted from [63].

populations. The rate of production of leaf biomass in eelgrass is an indicator variable for environmental influences on growth and also on the overall functions and values of this important seagrass species [29].

The forcing by environmental variables on the dynamics of *Z. marina* has been well documented in the literature [30–32]. Light availability, temperature and dissolved nutrients have been claimed as the most important variables for explaining the observed variability [29,33]. In particular, sea-surface temperature drives changes in aboveground biomass, and is highly correlated with leaf dynamics [29,34–36]. Hence even when light and nutrients are not limiting, temperatures beyond the upper limit of its tolerance range can provoke severe negative effects on eelgrass growth [37]. Global warming is expected to result in warming and rising seas, thus reducing the availability of both light and nutrients underwater [34]. Indeed, the onset of warm ENSO events has been shown to dramatically diminish eelgrass growth [37]. Another concern for the health of eelgrass populations is associated with deleterious anthropogenic influences. The loss of habitat for this macrophyte has been noted worldwide, with catastrophic losses within the past few decades [38–40]. These concerns have driven efforts aimed at preserving their populations, and several workers have relied on transplantation projects as a way to restore lost habitats [41–43,25].

Due to seasonality effects, the study of leaf growth in *Z. marina* demands extensive sampling during the entire yearly cycle. Tradi-

tional assessment methods require destructive and time consuming dry-weight determinations. The destruction of shoots during early stages of growth might provoke undesirable alterations in transplanted populations. To eliminate these inconveniences, we present a non-destructive and cost-effective method for the accurate estimation of growth rates, which uses an allometric model for the representation of leaf biomass in terms of the product of leaf length and width. The use of this construct could make the removal of shoots and the traditional dry-weight determinations unnecessary, and thus greatly simplifying conventional leaf-growth assessments including the plastochrone method [30,44].

## 2. Data and related variables

The primary data set used in this study was collected from April 1998 to April 1999 in a *Z. marina* meadow in the Punta Banda estuary, located near Ensenada, Baja California, Mexico. For a detailed description see [35]. Using the technique of Kentula and McIntire [45], we marked approximately 40 shoots at each sampling time  $t$ . At a date  $t + \Delta t$ , with  $\Delta t$  fixed at 2 weeks, we removed the marked shoots that were still present and marked a new sample. In what follows we will let  $l(t)$ ,  $h(t)$ ,  $a(t)$  and  $w(t)$ , respectively, denote length, maximum width, area and dry weight of a typical *Z. marina* leaf. For each one of the leaves on a recovered shoot, the corresponding  $l(t + \Delta t)$  values were directly obtained by measuring the distance between the ligula at the top of the sheath and the leaf tip. We also measured the leaf elongation increments  $\Delta l = l(t + \Delta t) - l(t)$  which are given by the displacement of the marking point from the ligula in the technique we used. Observations indicate that a typical *Z. marina* leaf has a long and narrow belted shape. This architecture can be explained by assuming that leaves grow initially both in a longitudinal and a transverse dimension, but while width quickly reaches a maximum value, length continues to increase towards an asymptotic value [29]. For a given maximum width, a great variability in corresponding leaf lengths has been observed. Hence we judged that measurements taken at a point halfway between the leaf tip and the ligula provided representative estimations for  $h(t + \Delta t)$ . This is consistent with other estimations of eelgrass leaf width reported in the literature, e.g., [46–48]. Following a customary approach, e.g., [49–54] we choose the product of  $l(t + \Delta t)$  and  $h(t + \Delta t)$  as a reasonable proxy value  $a_p(t + \Delta t)$  for the real leaf-area value  $a(t + \Delta t)$ . Moreover, for the biweekly marking interval considered, we also observed that an assumption of negligible values for  $\Delta h$  is fairly reasonable. Hence, we regarded the product  $h(t + \Delta t)\Delta l$  as a proxy value  $\Delta a_p$  for the real leaf-area increment  $\Delta a = a(t + \Delta t) - a(t)$ . The leaf biomass increments  $\Delta w = w(t + \Delta t) - w(t)$  associated with a leaf-area increment  $\Delta a$  were estimated through conventional procedures [44]. The observed values for  $\Delta w$  on a given shoot  $s$  were used to estimate the related mean rate of leaf growth over the interval  $(t, t + \Delta t)$ . These quantities are denoted here by means of the symbol  $L_{sg}(t, \Delta t)$  and formally defined through,

$$L_{sg}(t, \Delta t) = \frac{\sum_s \Delta w}{\Delta t}, \quad (1)$$

where  $\sum_s$  indicates summation over a given shoot. This notation convention, along with the use of a  $s$  subscript to label a generic shoot will be kept throughout.

The number of leaves produced by a shoot after it was marked was used to calculate the plastochrone interval using the formula in Jacobs [30]. These values were used to obtain alternative estimations for  $L_{sg}(t, \Delta t)$  according to the plastochrone method described in Gaekle and Short [44]. Finally, for our own and the plastochrone method determinations, we calculated the corresponding overall rates of leaf growth. These are referred to here by means

of the symbol  $L_g(t, \Delta t)$ , and obtained averaging the  $L_{sg}(t, \Delta t)$  values given by Eq. (1) over the number of collected shoots, i.e.,

$$L_g(t, \Delta t) = \frac{\sum_s L_{sg}(t, \Delta t)}{NS(t, \Delta t)}, \quad (2)$$

where  $NS(t, \Delta t)$  stands for the number of collected shoots.

In addition to the data presented in this study, we also used three other independent data sets for comparison purposes. The first, reported in Solana-Arellano et al. [55], was collected in San Quintin Bay during 1992–1993 and included lengths, widths and dry weights of complete leaves. A second data set, reported in Solana-Arellano [56] presented leaf lengths, widths and dry weights that were also obtained from our Punta Banda study site in 1999. Finally a third data set collected in 1987 in San Quintin Bay was obtained from Ibarra-Obando [57]. This includes plastochrone interval values, leaf lengths, widths, estimations for  $\Delta a$  and  $\Delta l$ , as well as observed values for corresponding  $L_g(t, \Delta t)$  rates.

### 3. Theoretical methods

Following Solana-Arellano et al. [58,59] we can show (see Eq. (A2)) that  $w(t)$  can be scaled in terms of  $a_p(t)$  through a model of the form,

$$w(t) = \rho a_p(t)^\alpha h(t)^\theta. \quad (3)$$

where  $\rho > 0$ , and  $\alpha$  and  $\theta$  are constants. It can also be shown (see Eqs. (A2)–(A5)) that, on the basis of the observed leaf architecture and growth form, we can derive from the above equation an allometric model for  $w(t)$  expressed solely in terms of  $a_p(t)$ . This is,

$$w(t) = c a_p(t)^m, \quad (4)$$

where  $c > 0$  and  $m$  are constants. Using this result, we can obtain indirect estimations for the corresponding leaf dry-weight increments  $\Delta w$  produced over the interval  $(t, t + \Delta t)$ . In fact, in a straightforward fashion from Eq. (4) we can obtain for  $\Delta w$

$$\Delta w = c a_p(t + \Delta t)^m \delta_p(t, \Delta t), \quad (5)$$

where the weighting factor  $\delta_p(t, \Delta t)$  is given by

$$\delta_p(t, \Delta t) = \left(1 - \left(1 - \frac{\Delta a_p}{a_p(t + \Delta t)}\right)^m\right). \quad (6)$$

The  $a_p(t + \Delta t)$  values can be directly obtained using measurements of leaf length and width on shoots collected. Since direct estimations for  $a_p(t)$  are unavailable, we must use leaf-marking data to produce these values. Indeed, the measured proxy values  $\Delta a_p$  will determine  $a_p(t)$  through the relationship  $a_p(t) = a_p(t + \Delta t) - \Delta a_p$ .

Adding the projected increments  $\Delta w$  on a given shoot and dividing by  $\Delta t$  we obtain projected values  $L_{psg}(t, \Delta t)$  for the observed mean leaf-growth rates  $L_{sg}(t, \Delta t)$  defined by Eq. (1) formally,

$$L_{psg}(t, \Delta t) = \frac{\sum_s c a_p(t + \Delta t)^m \delta_p(t, \Delta t)}{\Delta t}. \quad (7)$$

Averaging these values over the number of collected shoots we obtain a projected value  $L_{pg}(t, \Delta t)$  for the overall mean leaf growth  $L_g(t, \Delta t)$  defined by Eq. (2), e.g.,

$$L_{pg}(t, \Delta t) = \frac{\sum_s L_{psg}(t, \Delta t)}{NS(t, \Delta t)}. \quad (8)$$

It is worth pointing out that the reliability of the estimation given above depends on the consistency of the fitting of Eq. (4) to eelgrass data.

In Appendix we also show that there are suitable allometric constants  $b$  and  $k$  such that the result of Eq. (4) can be also

expressed directly in terms of the real leaf-area values  $a(t)$ , i.e., we also have

$$w = b a(t)^k, \quad (9)$$

for  $b > 0$  and  $k$  constants. Moreover, using the symbol  $L_{asg}(t, \Delta t)$  to denote projected leaf-growth rates expressed in terms of  $a(t)$ , we obtain (see Eqs. (A6)–(A12)),

$$L_{asg}(t, \Delta t) = \frac{\sum_s b a(t + \Delta t)^k \delta_a(t, \Delta t)}{\Delta t}, \quad (10)$$

where

$$\delta_a(t, \Delta t) = \left(1 - \frac{a(t)^k}{a(t + \Delta t)^k}\right). \quad (11)$$

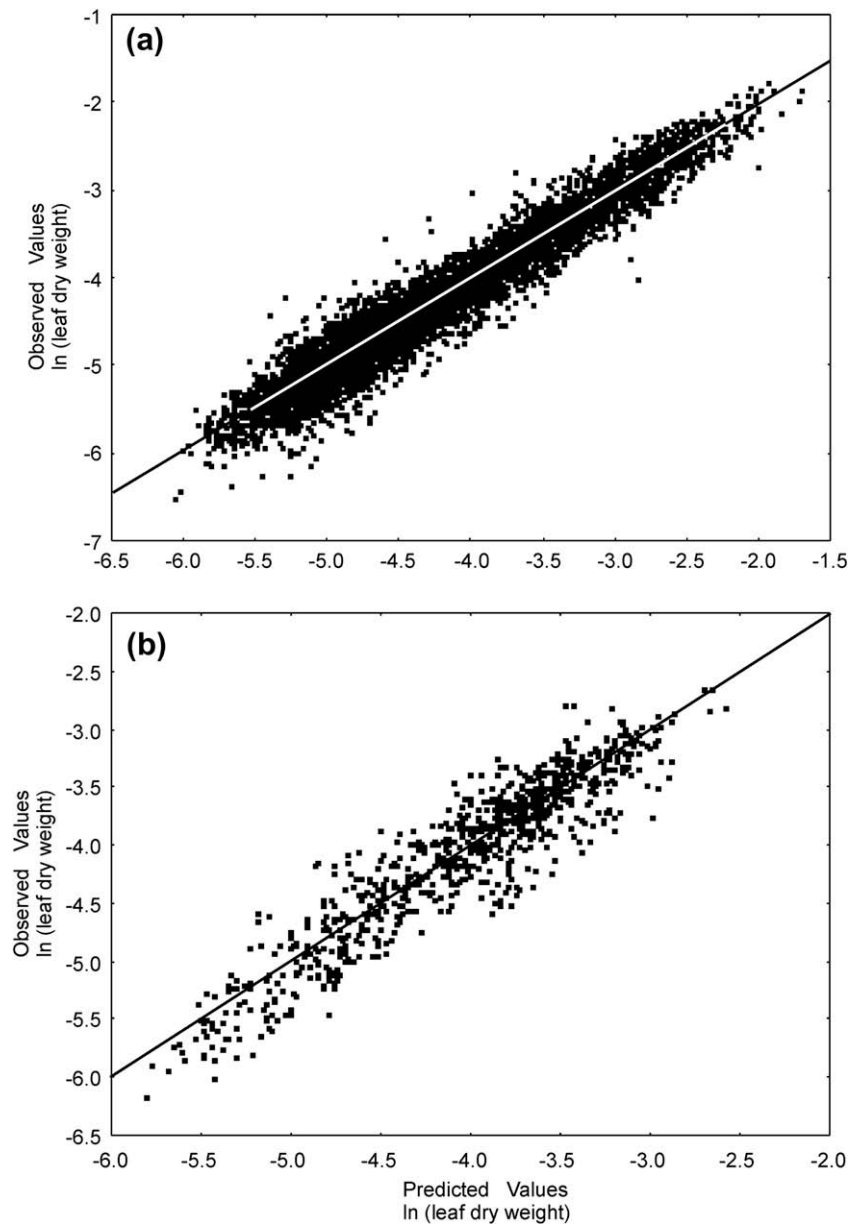
Moreover, this last estimation device does not require the use of leaf-marking techniques, which means a further simplification to the projection method given by Eq. (7). This last estimation device can be used whenever an automatic leaf-area meter is available. In such case we can produce direct and highly accurate estimations for  $a(t)$  [49].

### 4. Results

We fitted Eq. (3) to the Solana-Arellano et al. [55] data to obtain  $\rho = 0.000006$ ,  $\alpha = 1.24$ ,  $\theta = -0.44$  with a determination coefficients of  $R^2 = 0.93$ . The fit for the present data set produced  $\rho = 0.000004$ ,  $\alpha = 1.36$  and  $\theta = -0.61$  and  $R^2 = 0.87$ . Meanwhile, for the data reported in Solana-Arellano [56] we obtained  $\rho = 0.000004$  and  $\theta = -0.57$ ,  $\alpha = 1.44$  with  $R^2 = 0.95$ . Residual analyses for all these fittings showed that the residuals behave in accordance with the assumption of a general regression model, thus indicating that our model is consistent.

Using the above data sets, we also corroborated that eelgrass leaf architecture upholds a consistent identification of the simpler allometric model given by Eq. (4). The values for the parameters involved were  $c = 0.000004$  (std-err. = 0.02) and  $m = 1.21$  (std-err. = 0.003) with  $R^2 = 0.95$  for the Solana-Arellano et al. [55] records. For the present data set we found  $c = 0.000003$  (std-err. = 0.002) and  $m = 1.25$  (std-err. = 0.16) with a determination coefficients of  $R^2 = 0.92$ . Meanwhile for the Solana-Arellano [56] data we found  $c = 0.0000025$  (std-err. = 0.019),  $m = 1.3$  (std-err. = 0.15) and  $R^2 = 0.96$ . For all these fittings, the analysis of residuals shows consistency. The present data set and the Solana-Arellano et al. [55] are from different sites, so we judged it more informative to include in (Fig. 2) only the corresponding fittings.

Because the data for this study and that of Solana-Arellano [56] were obtained at the same study sites, we tested for differences in the allometric parameters  $c$  and  $m$  through time, and found no significant differences ( $p = 0.49$  for  $c$  and  $p = 0.71$  for  $m$ ). This suggests that, for our study site, a single representative sample including  $w(t)$  and  $a_p(t)$  values, will produce estimations of the parameters  $c$  and  $m$  that are expected to be valid through a complete yearly cycle of eelgrass growth. Moreover this property of time invariance in  $c$  and  $m$  might also be extended to data taken from a different study site. In fact, a test for statistical differences of fitted  $c$  and  $m$  values between the Solana-Arellano et al. [55] and the Solana-Arellano [56] data set also resulted in non-significant differences in allometric parameters between San Quintin Bay and the Punta Banda estuary ( $p = 0.50$  for  $c$  and  $p = 0.62$  for  $m$ ). The time span between these studies was 7 years. During these studies, different environmental conditions prevailed at the host sites (<http://www.cdc.noaa.gov/people.klauss.wolter/MEI>; <http://ferret.pmel.noaa.gov/NVODS/servlets/datasets>), but only negligible differences were noted in the fitted parameters. This indicates that



**Fig. 2.** Fittings of the allometric model  $w(t) = ca_p(t)^m$  (a) for the Solana-Arellano et al. [55] data ( $c = 0.000004$ ,  $m = 1.21$  and  $R^2 = 0.95$ ) and (b) for the present study data ( $c = 0.000003$ ,  $m = 1.25$  and  $R^2 = 0.92$ ).

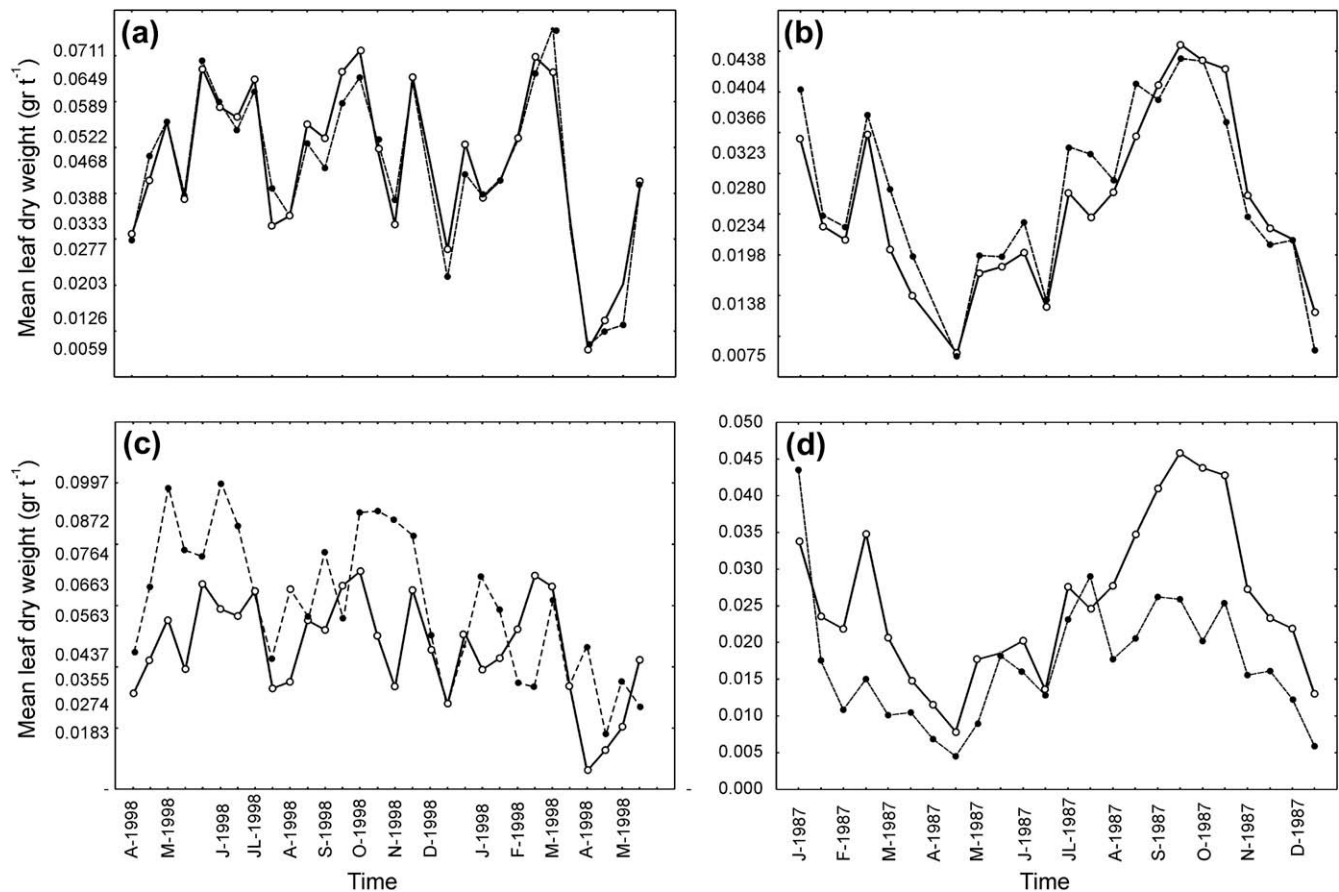
the assumption of time invariance for  $c$  and  $m$  in our study site could be extended to San Quintin Bay (which is approximately 100 km to the south). Moreover, we can also assume that parameters fitted to data sets taken at either of these sites – even during different years – could be used to project leaf-growth rates, for example in cases where the data required for the fitting of the model of Eq. (4) are missing. This criterion was used to produce projected values for leaf-growth rate from the data reported in Ibarra-Obando [57].

Once the parameters  $c$  and  $m$  were identified, we proceeded to apply our projection method (cf. Eq. (8)). We recall that for the Solana-Arellano [56] and Solana-Arellano et al. [55] data sets we could not obtain projected values  $L_{pg}(t, \Delta t)$  due to lack of estimated values for  $\Delta w$  and  $\Delta a$ . Fig. 3 displays a comparison of projected  $L_{pg}(t, \Delta t)$  and observed leaf-growth rates  $L_g(t)$  for the present and the Ibarra-Obando [57] data sets. For the latter data set we relied on parameter values  $c$  and  $m$  fitted from Solana-Arellano et al. [55]. The level of correspondence between projected and observed

values shown in Fig. 3(a) and (b) indicates that the results were trustworthy. This level of correspondence is remarkable if we compare with alternative assessments obtained by means of the named plastochrone method [30,44] (see Fig. 3(c) and (d)).

The robustness of our method was also explored through cross validation; that is, by interchanging fitted parameters. We projected the observed leaf-growth rates for the Punta Banda estuary using the parameters  $c$  and  $m$  fitted from the Solana-Arellano [56] data and compared those with the observed values reported here (Fig. 4(a)). Similarly we compared the above referred projections with those produced by our own data set (Fig. 4(b)). In the same manner, using  $c$  and  $m$  found for the San Quintin Bay data and reported in Solana-Arellano et al. [55] we projected leaf-growth rates for Punta Banda estuary and compared with projections obtained using the present data (Fig. 4(c)). Finally we projected leaf-growth rates for San Quintin Bay using  $c$  and  $m$  obtained from Punta Banda estuary data and compared with those projected using  $c$  and  $m$  fitted for the Solana Arellano et al. [55] data set (Fig. 4(d)). For an





**Fig. 3.** Plots of projected (dashed line) and observed (continuous line) mean leaf-growth rates through time. The plots on (a) and (b) correspond to values projected using Eq. (8). Panel (a) corresponds to the present data set. Panel (b) shows projections obtained using the Ibarra-Obando [57] data set. The plots on (c) and (d) represent mean leaf-growth rates obtained by means of the plastochrone method described in Jacobs [30] and Gaeckel and Short [44]. Panel (c) shows estimations for the present data set. Panel (d) displays assessments corresponding to the Ibarra-Obando [57] data.

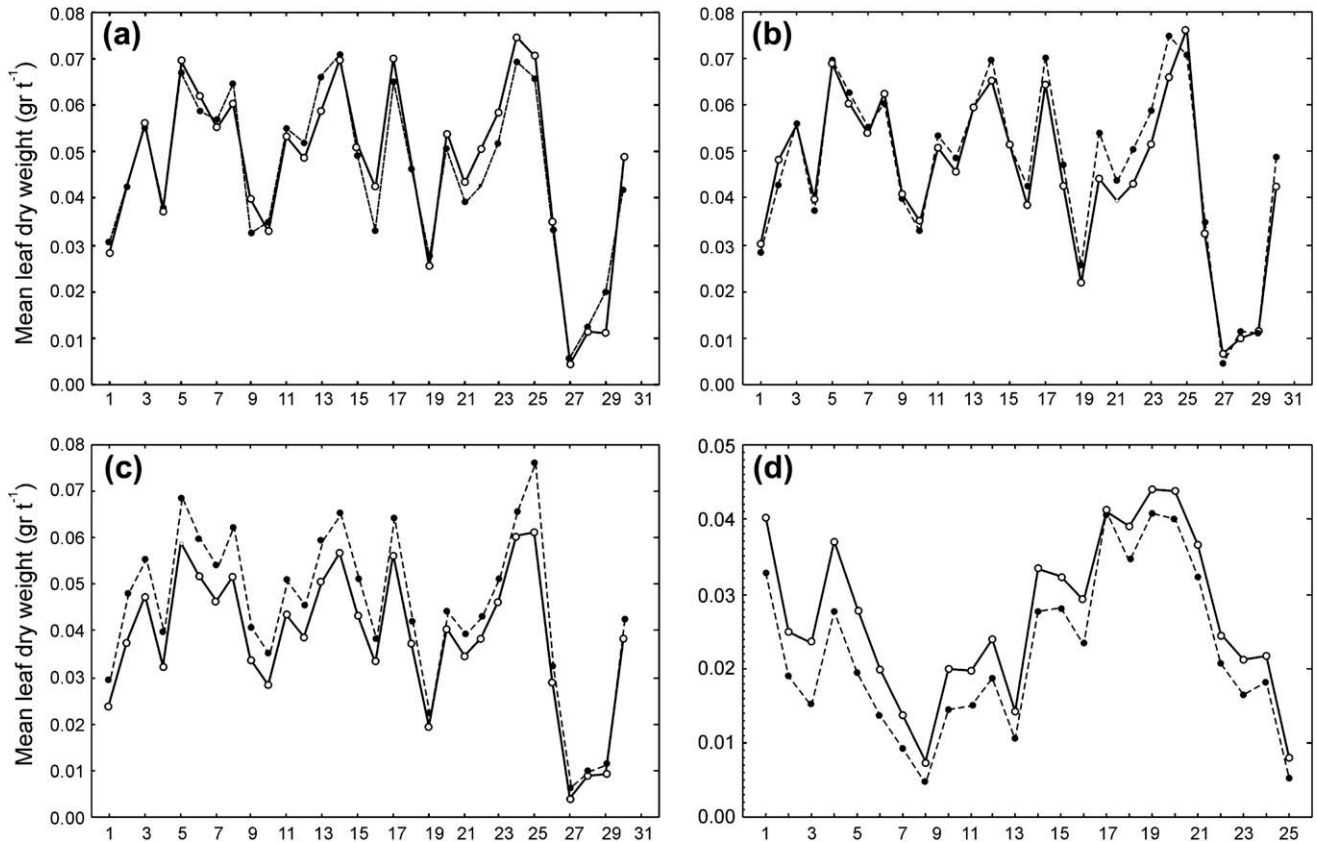
additional strength criterion, we tested for differences between observed and projected mean annual growth rates at each study site and for all projections, and found no significant differences ( $p > 0.09$  for all). This seems to indicate that, at each site, the observed mean annual growth rate is consistently represented by the corresponding projected values.

## 5. Discussion

The advantages of allometric relationships in seagrass research have been pointed out by several authors, e.g., [30,6,61,46,35]. In particular, for several pairs of representative  $X$  and  $Y$  seagrass variables, Duarte [62] found consistent representations of the form  $Y = \alpha X^\beta$  with  $\alpha$  and  $\beta$  constants. This study shows that eelgrass leaf architecture sustains the identification of a similar scaling relationship  $w(t) = ba(t)^k$  for leaf dry weight  $w(t)$  in terms of the area  $a(t)$ . Moreover, leaf-growth rates  $L_{pg}(t, \Delta t)$  derived from the model  $w(t) = ca_p(t)^m$  displayed significant levels of correspondence with observed values. When compared with pertinent assessments obtained by means of the plastochrone method, the proposed allometric approach turned out to be of greater accuracy. And the result of a test of non-significant differences for  $c$  and  $m$  using the referenced data sets suggests that these allometric parameters can be considered as time invariant. This means that a single representative sample of leaf areas and corresponding dry weights can be used to produce projections which are expected to be valid through a complete observation period. Moreover, we corroborated that parameter values can be interchanged among the sites considered, while still obtaining robust estimations. This suggests that the proposed allometric method can provide a simpler and more reliable non-destructive alternative for assessments of eelgrass leaf-growth rates. Because the estimation of leaf biomass production rates is an important input for assessing the status of eelgrass populations, the proposed method represents an added benefit of scaling relationships in eelgrass research. For example, in transplanted areas, determinations of leaf-growth rate are a fundamental entry to assess the restoration of ecological functions. A complete description of growth dynamics must consider estimations taken over the early stages of the transplant experiment, making it essential to rely on non-destructive methods. It is in this regard that our projection method could be most useful. In any case, our approach amounts to a reliable and cost-effective alternative to traditional or plastochrone-based determinations. Moreover, the  $L_{pg}(t, \Delta t)$  projections for the  $L_g(t, \Delta t)$  rates can be easily obtained, because the parameters  $c$  and  $m$  are derived from standard regression procedures and the  $a_p(t)$  values calculated from direct measurements of leaf lengths and widths and leaf-marking data.

The result of Eq. (9) shows that we can use other estimations of leaf area, different from  $a_p(t)$ , such as those produced by using an automatic leaf-area meter [48]. These estimations for  $a(t)$  are faster to obtain and may produce smaller approximation errors than those associated with  $a_p(t)$ . This procedure could also improve the quality of the fit of Eq. (9) over the one in Eq. (4), thereby resulting in more accurate projections. Because periods of low-tide

are common in eelgrass habitats, the use of an automatic leaf-area meter could be particularly useful. This procedure could also improve the quality of the fit of Eq. (9) over the one in Eq. (4), thereby resulting in more accurate projections. Because periods of low-tide



**Fig. 4.** Comparison of leaf-growth rates projected by means of Eq. (8) interchanging the parameters  $c$  and  $m$ . (a) Observed rates (dashed lines) and projected ones for the Punta Banda estuary using the Solana Arellano [56] data (continuous lines). (b) Rates projected for the Solana Arellano [56] data (dashed lines) and projections using the data set for the present study (continuous lines). (c) Rates projected with the present study data (dashed lines) and those projected for the same site but using the parameters  $c$  and  $m$  fitted for San Quintin Bay (i.e., using the Solana Arellano et al. [55] data (continuous lines)). (d) Rates projected for San Quintin Bay using data in Ibarra-Obando [57] with the parameters  $c$  and  $m$  fitted for Punta Banda (dashed lines) and projections for San Quintin using the Ibarra-Obando [57] data with the parameters  $c$  and  $m$  found from the fitting of the Solana Arellano et al. [55] data set (continuous line).

exposure are short, and plants may be submerged, it might be difficult to obtain a suitable number of replicates for  $a(t)$  through *in situ* measurements. Under these circumstances, one could rely solely on the leaf-marking approach described here. Even in the case in which one is limited to the use of leaf marking, our results show that reliable projected values for the  $L_g(t, \Delta t)$  rates can be obtained without the tedious dry-weight determinations of traditional or plastochrone assessment methods. The proposed model, moreover, can be applied to other seagrass species that have leaf architecture similar to eelgrass in a straightforward manner.

The results presented here raise the possibility that allometric parameters obtained at different sites and under different environmental conditions could be used in our paradigm to create independent and reliable projections of leaf-growth rates, thus amounting to a general, robust and non-destructive assessment method. The fact that the referenced data sets produce similar estimates for  $c$  and  $m$  suggest that this could be possible. Nevertheless, a generalization from the present results amounts to considering that  $c$  and  $m$  are species-specific properties and this must necessarily be substantiated by a larger data base, covering a larger range of distribution of eelgrass. This will be the subject of further research.

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## Appendix

Solana-Arellano et al. [58,59] generalized the model of Hamburg and Homann [46] and used independent data sets to corroborate that  $w(t)$  can be scaled by using an allometric model of the form,

$$w(t) = \rho l(t)^\alpha h(t)^\beta, \quad (\text{A1})$$

where  $\rho > 0$ ,  $\alpha$  and  $\beta$  are constants. We will show through that we can also express the above bivariate scaling of  $w(t)$  solely in terms of the considered proxy area  $a_p(t)$ . In order to obtain such a representation we first notice that Eq. (A1) takes the equivalent form,

$$w(t) = \rho a_p(t)^\alpha h(t)^\theta, \quad (\text{A2})$$

where  $\theta = \beta - \alpha$ . Now, let's consider a particular marked leaf. Then we will have  $w(t) > 0$ , and direct algebraic manipulation of Eq. (A2) yields,

$$\frac{w(t + \Delta t)}{w(t)} = \left( \frac{a_p(t + \Delta t)}{a_p(t)} \right)^\alpha \left( 1 + \frac{\Delta h}{h(t)} \right)^\theta. \quad (\text{A3})$$

Since we observed that during the chosen marking interval eelgrass leaf architecture and growth form resulting in negligible values for  $\Delta h$ , we might expect the ratio involving  $a_p(t)$  in Eq. (A3) to be dominant. On the other hand, if we assume that  $w(t)$  can be allometrically scaled in terms of  $a_p(t)$ , then, there will be a constant  $m$  [60] such that,

$$\frac{1}{w} \frac{dw}{dt} = \frac{m}{a_p} \frac{da_p}{dt},$$

and from this equation we obtain,

$$\frac{w(t + \Delta t)}{w(t)} = \frac{a_p(t + \Delta t)^m}{a_p(t)^m}. \quad (\text{A4})$$

Hence a dominance of the ratio involving  $a_p(t)$  in Eq. (A3) is consistent with the assumption of an allometric scaling of  $w(t)$  in terms of  $a_p(t)$ . Furthermore, assuming that Eq. (A4) holds for all  $t$  values, then both sides must be equal to a constant. Let  $c$  be such a constant. Then we will have

$$w(t) = ca_p(t)^m. \quad (\text{A5})$$

The result for  $\Delta w$  in the form of Eq. (A5) can be also obtained for leaf-area values  $a(t)$ . In fact, recalling that  $a_p(t)$  is an estimator for  $a(t)$  there must exist an approximation error  $\varepsilon_p(t)$  such that,

$$a(t) = a_p(t) + \varepsilon_p(t). \quad (\text{A6})$$

Moreover for the ratio

$$s(t) = \frac{\varepsilon_p(t)}{a(t)}, \quad (\text{A7})$$

an additional consistency condition

$$s(t) \ll 1, \quad (\text{A8})$$

is required.

Solving for  $a_p(t)$  in Eq. (A6) and replacing in Eq. (A5), we can obtain,

$$\frac{w(t + \Delta t)}{w(t)} = \left( \frac{a(t + \Delta t)}{a(t)} \right)^m \left( 1 - \frac{s(t + \Delta t) - s(t)}{1 - s(t)} \right)^m. \quad (\text{A9})$$

By virtue of the consistency condition in (A8), the right-hand side of Eq. (A9) will be dominated by the ratio  $a(t + \Delta t)^m a(t)^{-m}$ . Hence an elaboration such as the one used to establish Eq. (A5) will pertain, so we can also propose a general model, for eelgrass leaf dry weight  $w(t)$  and corresponding leaf-area values  $a(t)$ , e.g.,

$$w(t) = ba(t)^k, \quad (\text{A10})$$

where  $b$  and  $k$  are constants. In a manner like that established for Eq. (7) we can obtain an equation for the representation of projected rates  $L_{\text{asg}}(t, \Delta t)$  in terms of  $a(t)$  and the allometric parameters  $b$  and  $k$ , this will be,

$$L_{\text{asg}}(t, \Delta t) = \frac{\sum_s ba(t + \Delta t)^k \delta_a(t, \Delta t)}{\Delta t}, \quad (\text{A11})$$

where

$$\delta_a(t, \Delta t) = \left( 1 - \frac{a(t)^k}{a(t + \Delta t)^k} \right). \quad (\text{A12})$$

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